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Are farmed salmon more prone to risk than wild salmon? Susceptibility of juvenile farm, hybrid and wild Atlantic salmon *Salmo salar* L. to an artificial predator

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ABSTRACT

Offspring of farmed Atlantic salmon have been documented to display lower survival than the offspring of wild salmon in the wild. It has been suggested that reduced survival of farmed salmon offspring in the wild could, in part, be explained by increased susceptibility to predation through altered behaviour. This has however, not been demonstrated. This study investigated if farmed salmon display a higher susceptibility to predation than wild salmon, by exposing fry of farmed, hybrid and wild origin to an artificial predator in a semi-natural environment with competition for feed. The main results can be summarised as: (i) susceptibility to predation was similar in salmon of all origins, i.e., an equal number of farmed, hybrid and wild salmon were caught by the artificial predator; (ii) susceptibility to the artificial predator was not size-selective, i.e., large, fast growing individuals were caught in the same frequencies as small, slow growing individuals. As salmon fry of all origins were caught by the artificial predator in similar frequencies, equal susceptibility to predation was detected in farmed and wild salmon, under these conditions. If farmed salmon exhibit a genetically higher susceptibility to predation than wild salmon, potentially through increased risk-taking behaviour, this still remains to be demonstrated.

1. Introduction

Domestication selection for approximately ten generations has caused farmed Atlantic salmon *Salmo salar* L. to deviate from its wild counterpart in a broad range of traits (Einum and Fleming, 1997; Fleming and Einum, 1997; McGinnity et al., 1997, 2003; Gross, 1998; Thodesen et al., 1999; Skaala et al., 2004, 2005; Roberge et al., 2006, 2008; Glover et al., 2009; Houde et al., 2010a,b; Karlsson et al., 2011; Solberg et al., 2012, 2013a; Bicskei et al., 2014). In Norway, large numbers of farmed salmon escape from commercial fish farms every year (Norwegian Directorate of Fisheries, 2014). The majority of the escapees originate from large scale events where more than 10,000 fish escape at once (Jensen et al., 2010). As a consequence, the number of reported farmed escapees, in some years, even exceeds the number of wild salmon returning to the Norwegian coast (ICES, 2013). Due to hybridisation between farmed escapees and wild Atlantic salmon, the genetic integrity of wild populations is threatened (Skaala et al., 2006; Glover et al., 2012, 2013). Thus, successful conservation of wild populations requires a thorough understanding of the genetic differences between farmed salmon and their wild conspecifics.

Relaxed natural selection in the domestic environment combined with directional selection for production related traits, such as increased growth rate, has resulted in farmed

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salmon displaying reduced stress responsiveness (Solberg et al., 2013a), reduced predator awareness (Houde et al., 2010b), as well as increased aggressiveness and risk-taking behaviour (Einum and Fleming, 1997; Fleming and Einum, 1997; Houde et al., 2010a). This is in relation to wild Atlantic salmon, when kept together under hatchery or semi-natural conditions. Today, farmed Atlantic salmon outgrow wild salmon extensively when they are reared together in tanks (Gjedrem, 1979; Gjerde, 1986; Einum and Fleming, 1997; Thodesen et al., 1999; Fleming et al., 2002; Glover et al., 2009; Solberg et al., 2013a). In strong contrast, only small to modest differences in growth are observed between the offspring of farmed and wild salmon when planted out in the wild as eggs (Skaala et al., 2012) or released as parr (Fleming et al., 2000).

In a previous study performed under hatchery and semi-natural conditions, we demonstrated that the relative differences in growth between wild and farmed juvenile salmon decreased along an environmental gradient approaching more natural conditions (Solberg et al., 2013b). However, the most natural conditions included in that study, which was conducted in the period between egg hatching and the fry stage, only included a semi-natural habitat with hiding places and competition for food. If however, a predator had been present, potentially selecting fast-growing and potentially risk-taking individuals as prey, a further decrease in growth differences between wild and farmed salmon may have been detected. That is, if the documented reduced predator awareness (Houde et al., 2010b) and increased risk-taking behaviour (Einum and Fleming, 1997; Fleming and Einum, 1997; Houde et al., 2010a) in farmed salmon is linked with increased susceptibility to predation.

The offspring of farmed salmon display a lower survival than the offspring of wild salmon in nature, i.e., lower recapture rates after being released in the wild (McGinnity et al., 1997; Fleming et al., 2000; McGinnity et al., 2003; Skaala et al., 2012). In the above studies, offspring of farmed and wild salmon were compared in the same natural environment and at the same time. Thus, the reduced survival in farmed salmon could be explained by farmed salmon displaying a genetically higher susceptibility to predation, potentially linked with a higher predisposition to risk taking behaviour (Einum and Fleming, 1997; Fleming and Einum, 1997). In a recent study, performed in the river Guddal, Norway, susceptibility of farmed, hybrid and wild salmon to predation by brown trout (*Salmo truttta* L.) was investigated (Skaala et al., 2014). In that study, salmon of all origins were equally predated upon (Skaala et al., 2014). However, there are several challenges in investigating predation of different genetic groups in the wild, and there is still a need to investigate this under more controlled conditions.

If the offspring of farmed salmon exhibit a genetically higher susceptibility to predation than the offspring of wild salmon, through altered risk-taking behaviour, this has yet to be demonstrated. Therefore, the primary objective of the present study was to investigate if the offspring of farmed salmon display a higher susceptibility to predation as compared to the offspring of wild salmon in a controlled semi-natural environment where competition for feed is high. In order to identify risk taking individuals, a neutral artificial predator, i.e., a large handling net, was placed underneath the feeding station. The artificial predator was then activated after a warning signal was given, allowing fish to escape the area before the net was pulled out of the water. The rationale behind the artificial predator system was that any individual remaining in the area after the warning signal was given was prioritising feeding behaviour instead of anti-predator behaviour, thus displaying increased risk-taking behaviour. Additionally, we aimed to investigate whether faster growing individuals in general displayed a higher susceptibility to predation than slow growing individuals, i.e., increased risk-taking behaviour. If fast growing farmed individuals were caught by the artificial predator more frequently than more slowly growing farmed individuals, the relative weight of farmed and wild salmon should appear more similar post exposure to the artificial predator than prior to. For that reason, individual weight and length measurements were collected prior to and post the experimental period, and matched by the use of individual DNA profiling.

2. Methods

2.1. Overall design

In order to elucidate behavioural susceptibility to predation in wild, F_1 hybrid and domesticated Atlantic salmon at the juvenile stage; young-of-the-year salmon (0+) that had been produced under identical hatchery conditions were in autumn 2011 placed in a semi-natural environment for three weeks. The environment contained hiding places, competition for access to feed, and an artificial predator. This environment was established to invoke competition for access to food, with the trade-off for risk of being predated upon. For a schematic overview of the experiment, see Fig. 1.

2.2. Experimental crosses and rearing

Wild Atlantic salmon caught in the Norwegian river Figgjo (58°81′ N, 5°55′ E), and farmed salmon originating from the commercial Mowi strain were in 2010 used to generate three experimental F_1 crosses for this study: (i) nine pure wild families; (ii) ten pure farmed families; and (iii) ten F_1 hybrid families, generated by crossing farmed females with wild males. Thus the hybrid families were maternal and paternal half siblings of the farmed and wild families, respectively. The three experimental strains are from hereon referred to as farmed (Mowi), hybrid (Mowi × Figgjo) and wild (Figgjo). The strains were reared separately under identical standard farming conditions from the eyed egg stage in February 2011, until the fish were selected for the present experiment at the fry stage in October 2011. In this period, the fish were fed a commercial fish pellet diet ad lib. in order to provide maximum growth rates in all groups.

2.3. Experimental conditions and sampling

The experiment was initiated on 10 October 2011. On this day, a total of 120 fish per strain were randomly

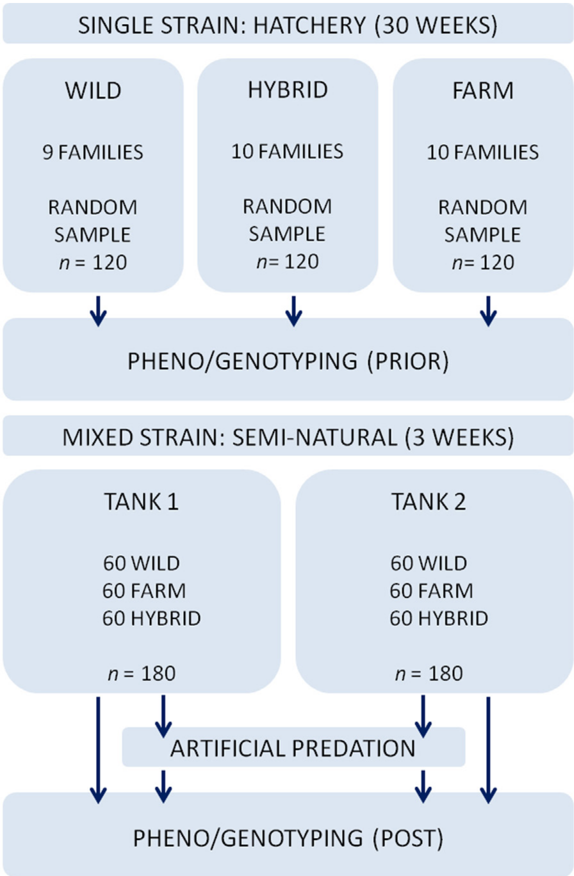

Fig. 1. Overview of the experimental design. Atlantic salmon *Salmo salar* L. of all origins was reared from the eyed-egg stage in February 2011 until October 2011, i.e., for 33 weeks, under standard hatchery conditions in single-strain mixed-family tanks. Then 120 individuals per strain (across two replicates) were sorted out for this common-garden experiment, and mixed in a semi-natural environment. The experimental period in mixed-strain mixed-family tanks lasted for three weeks, and the 360 individuals were in this period exposed to competition for feed and an artificial predator (twice a day, five days a week). The artificial predator was initiated after one week of acclimatisation to the semi-natural environment with restricted access to feed. Individual growth measurements were collected prior to and post the experimental period and matched by the use of individual DNA profiling. All individuals caught by the artificial predator or that died of undefined causes were collected and temporarily stored at −20 °C until the experiment was terminated.

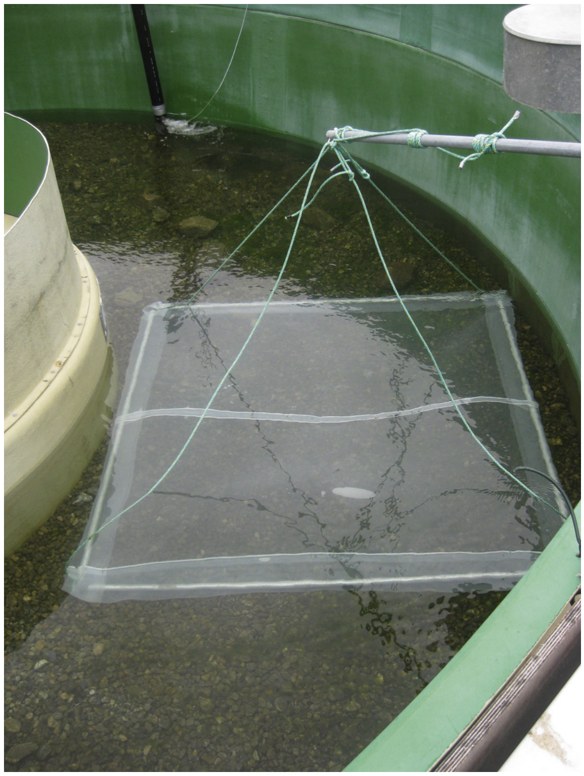

Fig. 2. The artificial predator. The artificial predator, a 2 m × 1.8 m handling net, was permanently located underneath the single feeding station for each tank. A restricted feed ration, 25% of the ration recommended by the commercial industry, was provided from 08:30 to 20:30 each day. Twice a day, at 09:00 and 14:00, five days a week, the artificial predator was manually activated. First, a signal of danger was given, i.e., a splash in the middle of the net, induced by a small stone being thrown into the water from above. Then, with a delay of approximately 2 s, the handling net was quickly pulled out of the water, and individuals caught by the net were euthanised and temporarily stored at −20 °C. Salmon fry were given one week to acclimatise to the semi-natural environment with competition for feed, before the artificial predator was active for two weeks, i.e., ten days in total.

selected from the 3 single strain tanks. All 360 fish were anesthetised before wet weight and fork length was taken. At the same time, all 360 fish were adipose fin clipped for later DNA analysis. Thereafter, 60 fish per strain were randomly mixed into two semi-natural tanks (thus 180 fish per tank, 60 wild, 60 hybrid and 60 farmed). In the semi-natural environment, a restricted feed ration was provided. This was in order to create competition for this resource (25% of the ration recommended by the commercial industry was given).

The semi-natural environment consisted of two c. 31.4 m^2 circular shaped passages filled with gravel and hiding places (outer radius 3.5 m, inner radius 1.5 m), where the water level and velocity were modified according to the levels documented at spawning areas of Atlantic salmon (Barlaup et al., 2008). An automatic feeder was placed immediately beside the water inlet in each of the two replicate tanks. This provided a single point source for the feed. Feed was provided 12 h per day, from 08:30 to 20:30. Twice a day (at 09:00 and 14:00), five days a week, an artificial predator (a 2 m × 1.8 m handling net permanently located underneath the single feeding station in each replicate tank) was manually activated after giving a signal of danger (a splash in the middle of the net, induced by a small stone being thrown into the water from above) (Fig. 2). With a delay of approximately 2 s, the handling net was quickly pulled out of the water, in order to capture individuals that were still in the feeding area and not responding to the signal. All individuals caught by the net were euthanised and temporarily stored at −20 °C. The semi-natural environment was located outside and thus subjected to natural light. However, additional light was provided during the 12 h feeding period.

Salmon were given one week to acclimatise to the semi-natural environment before the artificial predator was activated on day 7. After two weeks of exposure to the artificial predator, i.e., 10 days in total, the experiment was terminated October 31, 2011, on day 21. Thus the overall experimental period lasted for three weeks.

At termination, all individuals remaining in the semi-natural environment were euthanised, while frozen individuals, i.e., individuals that either was caught by the artificial predator or died of undefined causes during the experimental period, were thawed. Weight and fork length was thereafter measured for all individuals. In addition, the caudal fin was clipped for all individuals to provide a tissue for DNA analysis. For frozen/thawed individuals, an expected reduction in length and weight of 3.2% and 4.5%, respectively, were controlled for (Sutton et al., 2000).

2.4. Genotyping and parentage testing

Microsatellite DNA profiling of the adipose fin clip samples (start of experiment) and the caudal fin clip samples (termination of the experiment) was used to connect the weight measurements of the fish between the start and termination of the experiment (i.e., individual DNA profiling). DNA was extracted in 96 well plates using a Qiagen DNeasy®96 Blood & Tissue Kit. Two randomly assigned blank wells were included on each plate as a negative control. In one multiplex PCR, six microsatellite loci were amplified; *SsaF43* (Sánchez et al., 1996), *Ssa197* (O'Reilly et al., 1996), *SSsp3016* [GenBank# AY372820], *MHCI* (Grimholt et al., 2002), *MHCII* (Stet et al., 2002) and *SsOSL85* (Slettan et al., 1995). For individuals displaying identical genotype combinations to other fish after genotyping with the first multiplex of six markers, a second multiplex including five more loci was amplified; *Sp1605* (Paterson et al., 2004), *Sp2216* (Paterson et al., 2004), *Ssa14* (McConnell et al., 1995), *Ssa171* (O'Reilly et al., 1996) and *Ssa289* (McConnell et al., 1995). PCR products were run on an ABI Applied ABI 3730 Genetic Analyser Biosystems and sized-called according to the 500LIZ™ standard. Genotypes were identified using GeneMapper V4.0 with manual control of scored alleles, and assigned to family by the use of FAP Family Analysis Programme v3.6 (Taggart, 2007). FAP utilises an exclusion-based approach to unambiguously identify parental origin, and has been successfully used on several occasions for parentage testing common-garden studies using these facilities (Glover et al., 2001, 2004; Solberg et al., 2012, 2013a,b). In order to verify genotyping quality, 14 samples were randomly selected for re-genotyping, where all gave identical genotype and parentage assignment on the second analysis.

2.5. Ethical approval

This study complies with the International Guiding Principles for Biomedical Research Involving Animals (2012) as issued by the Council for International Organisation of Medical Sciences (CIOMS) and the International Council for Laboratory Animal Science (ICLAS), and the Guidelines for the ethical use of animals in applied ethology studies (Sherwin et al., 2003). The experimental protocol (permit number 3797) was approved September 26, 2011, by the Norwegian Animal Research Authority (NARA). Welfare and use of experimental animals was performed in strict accordance with the Norwegian Animal Welfare Act.

2.6. Statistical analysis

All statistical analyses were performed using R version 3.1.0 (R Core Team, 2014), with critical *P*-values set to 0.05.

In order to investigate if the initial body weight (Y) varied between strains, i.e., farmed, hybrid and wild salmon, and furthermore influenced the individuals destiny, i.e., survived the experimental period, was caught by the artificial predator in the morning, was caught by the artificial predator in the afternoon or died of undefined causes; a linear mixed effect (LME) model was fitted using the *lmer* function in the lme4 package (Bates et al., 2014). The full model was fitted with strain (S) and destiny (D) as fixed effects and tank (t) and family (f) as random intercept factors, thus allowing for heterogeneity of variance;

$$Y = \alpha + \beta_1 S + \beta_2 D + b_t + b_f + \varepsilon \tag{1.1}$$

where α is the intercept and ε is a random error. Normality of the distribution of the model residuals was investigated graphically by the use of histograms. Model selection was performed backwards by the use of the *step* function in the lmerTest package (Kuznetsova et al., 2014). By this procedure, insignificant random effects were eliminated, followed by the removal of insignificant fixed effects (potential interaction terms before the variables themselves). *F*-statistics, denominator degrees of freedom and *P*-values calculated based on Satterthwaite's approximations were presented for the fixed effects, while P-values for the random effects were calculated based upon likelihood ratio tests (Kuznetsova et al., 2014). For the fixed effects, least squares means and differences of least squares means were calculated, i.e., parameter level tests. For significance levels of the random and fixed effects of the full LME model 1.1, see Table 1. The interaction term between strain and destiny were not included in model 1.1 as this resulted in the model matrix being rank deficient, i.e., only wild salmon died of undefined causes during the experiment thus not all combinations of factor levels were present. Therefore, a similar LME model including the interaction term between strain and destiny were fitted after removing these eight dead individuals from the data set;

$$Y = \alpha + \beta_1 S + \beta_2 D + \beta_3 SD + b_t + b_f + \varepsilon \tag{1.2}$$

where α is the intercept and ε is a random error. Model selection was performed in the same manner as described above. For significance levels of the random and fixed effects of the full LME model 1.2, see Table 1.

In order to investigate the influence of strain upon susceptibility to the artificial predator, a generalised linear mixed effect model (GLMM) was fitted using the *glmer* function in the lme4 package (Bates et al., 2014). The wild individuals that died of undefined causes were not included in the model. The full model tested for the effect of strain (S) and initial weight (W), as well as their interaction, upon susceptibility to the artificial predator (Y), while tank (t) and family (f) were included as random intercept factors;

$$\log it(Y) = \alpha + \beta_1 S + \beta_2 W + \beta_3 SW + b_t + b_f + \varepsilon \tag{2}$$

Table 1
Significance levels of random and fixed effects included in the full LME models investigating variation in initial weight and growth of farmed, hybrid and wild salmon.

Model	N	Response	Random effects				Fixed effects					
			Variable	Chi.sq	Chi.Df	P	Variable	Sum.sq	NumDf	DenDf	F	P
1.1	360	Initial weight	Tank	0.2	1	0.7	Strain	11,234.2	2	26	117.4	**<0.0001**
			Family	17.6	1	**<0.0001**	Destiny	1034.4	3	345	3.7	**0.01**
1.2	352	Initial weight	Tank	0.0	1	0.9	Strain × destiny	261.5	4	333	1.3	0.25
			Family	17.7	1	**<0.0001**	Strain	11,757.9	2	27	120.0	**<0.0001**
							Destiny	160.1	2	337	1.2	0.30
3	315	Ω	Tank	4.8	1	**0.03**	Strain	3.2	2	25	2.7	0.09
			Family	17.2	1	**<0.0001**						

Model selection of the linear mixed effect models investigating variation in initial weight and growth of farmed, hybrid and wild Atlantic salmon. Initial weight, wet weight prior to the experimental period (gram). Ω, standardised mass-specific growth rate, % per day (only surviving individuals). Random effects: tank: (1) replicate one, (2) replicate two. Family: 10:10:9, farm, hybrid, wild families, respectively. Chi.sq, value of the Chi square statistics. Chi.Df, the degrees of freedom for the test. *P*, *p*-value of the likelihood ratio test for the random effect. Fixed effects: strain: (1) farm, (2) hybrid, (3) wild. Destiny: (1) survived the experimental period, (2) caught by artificial predator in the morning, (3) caught by the artificial predator in the afternoon, (4) died of undefined causes. Sum.sq, sums of squares; Num.Df, numerator degrees of freedom; Den.Df, denominator degrees of freedom (Satterthwaite's approximation); *F*, *F*-value; *P*, *p*-value. The eight wild individuals that died of undefined causes during the experimental period were not included in model 1.2, this in order to investigate the interaction between strain and destiny. Significant effects are marked in bold.

where α is the intercept and ε is a random error. Due to survival being binary data the binomial distribution was selected with a logistic link function and the model was fitted using the Laplace approximation. The significance level of the random effects were assessed by fitting the full model while only including one random effect at a time, before plotting the 95% prediction intervals of the random effect, using the *dotplot* function of the lattice package (Deepayan, 2008). As all of the prediction intervals of the random effects overlapped zero, they were considered non-significant. Thus a generalised linear model (GLM) was fitted, and further elimination of insignificant fixed effects was performed by the *drop1* function which applies a likelihood ratio test that is Chi-squared distributed. For significance levels of the fixed effects included in the full GLM model 2, see Table 2.

In order to quantify growth during the experimental period in surviving salmon, while controlling for variation in body size between salmon of farmed and wild origin, the standardised mass-specific growth rate Ω (% per day) was calculated for each individual, following Ostrovsky (1995):

$$\Omega = \frac{M_t^b - M_0^b}{bt} \times 100$$

M_0 and M_t is the wet weight prior to and post the experimental period, respectively, t is the number of days individuals were allowed to grow between the weight measurements, i.e., 21 days, and b is the species-specific allometric mass exponent describing the relationship between growth rate and body mass. For juvenile Atlantic salmon b is estimated to be 0.31 (Elliott and Hurley, 1997). In order to investigate if Ω varied between surviving salmon of farmed, hybrid and wild origin a linear mixed effects (LME) models were fitted using the *lmer* function in the lme4 package (Bates et al., 2014). The initial full model was thus fitted to investigate the effect of strain (S) upon Ω (Y). Tank (t) and families (f) were included as random intercept factors;

$$Y = \alpha + \beta_1 S + b_t + b_f + \varepsilon \quad (3)$$

where α is the intercept and ε is a random error. Model selection was performed in the same manner as described above. For significance levels of the random and fixed effects of the full LME model 3, see Table 1.

3. Results

3.1. Mortality, sampling and genotyping

Out of the 360 individuals included in this study, 31 individuals were caught by the artificial predator in the morning (09:00), six individuals were caught in the afternoon (14:00), seven individuals died of undefined

Table 2
Significance levels of the fixed effects included in the full GLM investigating variation in susceptibility of farmed, hybrid and wild salmon to the artificial predator.

Model	N	Response	Term	Remove	DF	Deviance	AIC	LRT	P
2	352	Susceptibility	Initial weight × strain	None		234.2	246.2		
				Strain × initial weight	2.0	235.1	243.1	0.86	0.6
				Strain	2.0	235.9	239.9	0.79	0.7
				Initial weight	1.0	236.7	238.7	0.79	0.4

Model selection of the generalised linear model investigating variation in susceptibility to the artificial predator between farmed, hybrid and wild Atlantic salmon *Salmo salar* L. Susceptibility: (1) not caught by the artificial predator, (2) caught by the artificial predator. Strain: (1) farm, (2) hybrid, (3) wild. Initial weight: wet weight prior to the experimental period (gram). Df, degrees of freedom; AIC, Akaike's information criterion; LRT, likelihood ratio test; *P*, LRT test *p*-value. Initially a generalised liner mixed effect model (GLMM) was fitted with tank and family as random intercept factors, but as the random effects were assessed to be insignificant, a simpler GLM were fitted only including fixed effects.

Table 3
Growth measurements of Atlantic salmon *Salmo salar* L. of farmed, hybrid and wild origin.

Treatment	Group	Tank	*n*	Pre-experimental measurements						Post-experimental measurements							
				W (g)		*L* (cm)		*K*		*W* (g)		*L* (cm)		*K*		*Ω*	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Survived	Farm	1	54	33.28	9.58	13.32	1.38	1.36	0.08	31.20	8.52	13.61	1.42	1.21	0.20	−0.85	0.94
		2	54	39.80	8.99	14.16	1.10	1.38	0.07	36.54	8.23	14.49	1.09	1.18	0.05	−1.24	0.78
	Hybrid	1	54	25.41	6.97	12.14	1.21	1.38	0.07	23.50	6.68	12.49	1.23	1.17	0.06	−1.02	0.75
		2	53	24.36	5.87	12.14	1.21	1.35	0.13	22.09	5.57	12.35	1.09	1.15	0.07	−1.25	0.80
	Wild	1	53	13.02	5.85	9.73	1.58	1.31	0.10	11.77	5.64	9.87	1.64	1.12	0.10	−1.16	0.79
		2	47	10.89	4.37	9.22	1.17	1.32	0.11	9.36	4.11	9.33	1.30	1.08	0.13	−1.57	0.97
Sampled 09.00	Farm	1	5	31.40	5.94	13.04	0.70	1.40	0.08	30.60	4.39	13.10	0.65	1.35	0.03	−0.64	2.04
		2	5	35.20	11.65	13.52	1.56	1.38	0.05	34.60	10.69	13.63	1.51	1.33	0.04	−0.15	1.06
	Hybrid	1	5	20.80	4.66	11.46	0.85	1.36	0.06	19.80	4.87	11.57	0.95	1.25	0.09	−1.34	1.06
		2	6	21.67	4.18	11.77	0.77	1.32	0.07	21.83	3.76	11.80	0.77	1.32	0.03	0.34	0.97
	Wild	1	2	10.50	6.36	9.25	1.77	1.23	0.09	11.00	7.07	9.35	1.82	1.25	0.07	0.74	0.10
		2	8	13.88	5.25	9.98	1.38	1.33	0.04	13.13	5.44	9.93	1.53	1.27	0.14	−1.28	1.23
Sampled 14.00	Farm	1	1	24.00	NA	12.1	NA	1.35	NA	24	NA	12.29	NA	1.30	NA	0.09	NA
		2	1	44.00	NA	14.70	NA	1.39	NA	43.00	NA	14.77	NA	1.33	NA	−0.79	NA
	Hybrid	1	1	40.00	NA	14.50	NA	1.31	NA	38.00	NA	14.46	NA	1.25	NA	−1.84	NA
		2	1	23.00	NA	11.50	NA	1.51	NA	21.00	NA	11.67	NA	1.32	NA	−2.44	NA
	Wild	1	1	14.00	NA	10.10	NA	1.36	NA	14.00	NA	10.54	NA	1.16	NA	−0.79	NA
		2	1	4.00	NA	6.50	NA	1.46	NA	3.00	NA	6.51	NA	1.14	NA	−3.58	NA
Died	Wild	1	4	3.75	1.50	6.80	0.75	1.15	0.10	3.33	1.53	6.13	1.00	1.31	0.07	−4.82	6.51
		2	4	5.00	1.15	7.35	0.90	1.27	0.21	4.39	0.95	6.91	0.73	1.33	0.16	−2.01	1.86

W, wet weight; *L*, fork length; *K*, condition factor; *Ω*, standardised mass-specific growth rate, % per day. Individuals that were caught by the artificial predator, or that died during the experimental period were frozen and thawed before the post-experimental measurements were taken. We expected freezing to reduce the length and weight by 3.2% and 4.5%, respectively (Sutton et al., 2000). Hence, the post experimental measurements were adjusted in all individuals that had been frozen. One individual in tank 1 was not detected at the time of termination, and therefore assumed dead. Hence the pre-experimental measurements of dead individuals in this tank were based upon four individuals, while the post-experimental measurements were based upon three individuals.

causes during the experiment, while one individual was not detected at the time of termination and therefore assumed dead (Table 3, Fig. 3). All eight individuals that died of undefined causes were of wild origin (Table 3, Fig. 3) and were detected/registered on day 0, 4, 7, 8, 11 and 21 of the experimental period. Thus, 315 surviving individuals were collected when the experiment was terminated.

All 359 salmon detected at the end of the experiment, including their biological data taken prior to and post the experimental period, were successfully identified using DNA. 357 individuals were identified using individual DNA-profiling, while two individuals were identified by their individual length measurements. For four individuals the adipose fin sample taken before the experiment was initiated was too small for successful DNA extraction. Two of these individuals, one wild and one hybrid, were still identified by DNA-profiling as strain of origin were known prior to the experimental period. The remaining two individuals were of farmed origin, and were identified by their morphological measurements. This was possible due to one individual being shorter than the other.

3.2. Initial weight prior to the experimental period

Farmed salmon were significantly larger than hybrid salmon, which again were significantly larger than wild salmon (Tables 3 and 4, Fig. 4). Taking strain into

Table 4
Parameter level tests for the fixed part of the final LME model investigating difference in initial weight between salmon strains and destinies.

Model	Response	Variable	Factor levels	*N*	Estimate	SE	DF	*t*-value	Lower CI	Upper CI	*P*
1.1	Initial weight	Strain	Farm vs. hybrid	240	11.4	1.5	26.5	7.5	8.3	14.5	**<0.0001**
			Farm vs. wild	240	24.1	1.6	26.4	15.3	20.8	27.3	**<0.0001**
			Hybrid vs. wild	240	12.7	1.6	25.9	8.2	9.5	15.9	**<0.0001**
		Destiny	Sampled 09.00 vs. sampled 14.00	37	−1.1	3.2	342.8	−0.3	−7.3	5.1	0.73
			Sampled 09.00 vs. survived	346	−2.1	1.3	346.3	−1.5	−4.7	0.6	0.13
			Sampled 14.00 vs. survived	321	−1	2.9	341.7	−0.3	−6.7	4.7	0.74
			Died vs. sampled 09.00	39	−5.9	2.9	345.6	−2.0	−11.6	−0.2	**0.04**
			Died vs. sampled 14.00	14	−7	3.9	342.8	−1.8	−14.6	0.6	0.07
			Died vs. survived	323	−7.9	2.6	346.1	−3.0	−13.1	−2.8	**0.003**

Differences of least squares means for the fixed part of the final LME model investigating difference in initial weight prior to the experimental period in farmed, hybrid and wild Atlantic salmon *Salmo salar* L. exposed to competition for feed and an artificial predator. SE, standard error; Df, degrees of freedom; CI, confidence intervals. Significant results are marked in bold. Differences of least squares means between significant fixed effects in model 1.2 where dead individuals were excluded, i.e., only strain, displayed the same significance levels as model 1.1. These results are therefore not presented.

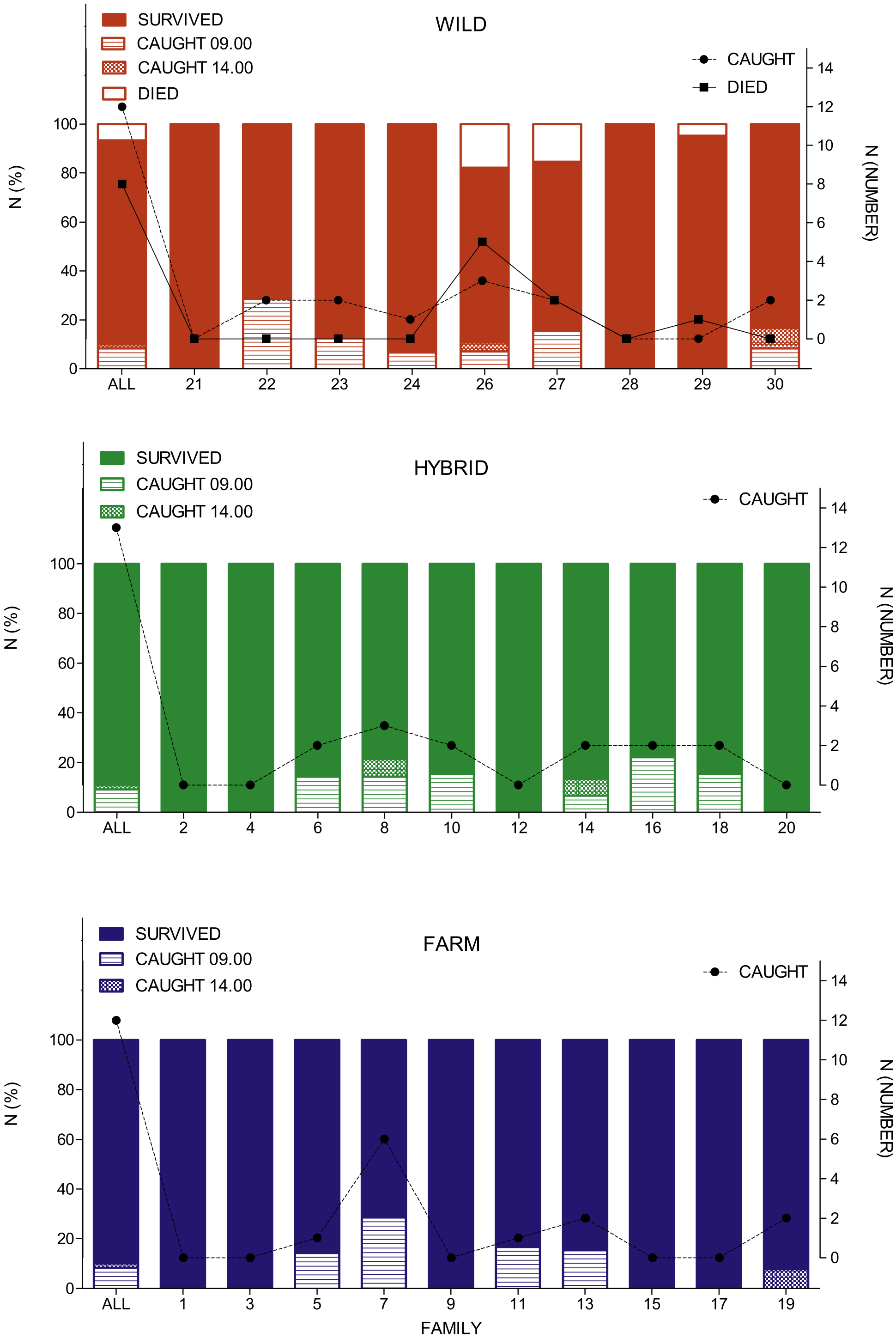

Fig. 3. Numbers caught by the artificial predator. Atlantic salmon *Salmo salar* L. individuals, percent (bars) and numbers (dotted line) per strain and family, that survived the three week experimental period, were caught by the artificial predator in the morning, caught in the afternoon or that died of undefined causes during the experimental period. A total of 360 individuals, 120 farmed, hybrid and wild salmon, respectively, were included in this common-garden study. 315 individuals survived the experimental period, 31 individuals were caught by the artificial predator in the morning, six individuals were caught by the artificial predator in the afternoon, while eight wild individuals died of undefined causes. Farmed, hybrid and wild individuals were caught in similar frequencies by the artificial predator both in the morning and in the afternoon, i.e., 10:11:10, and 2:2:2, respectively.

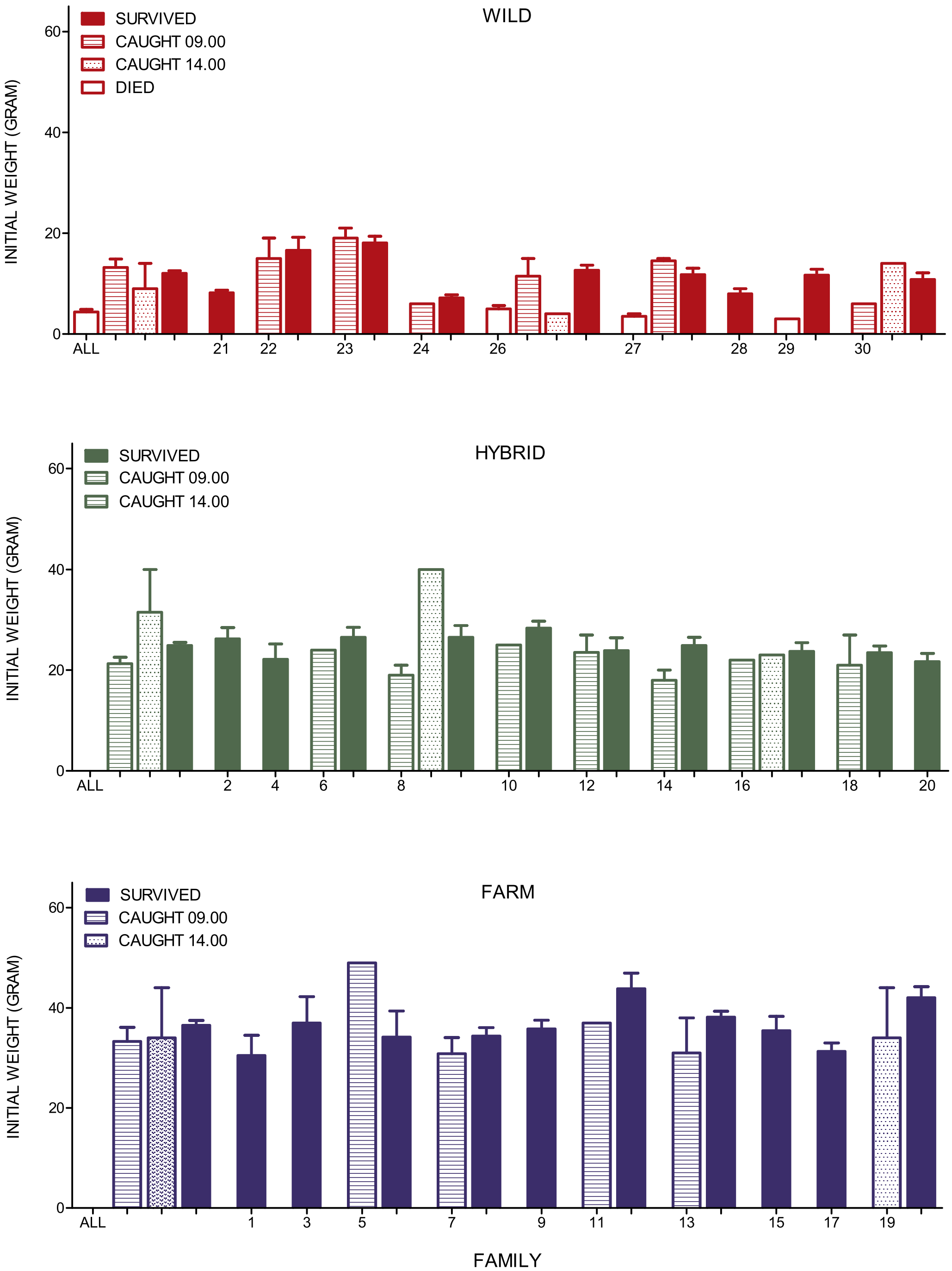

Fig. 4. Mean initial weight of wild, hybrid and farmed salmon. Mean strain and family weight prior to the experimental period of the wild, hybrid or farmed Atlantic salmon *Salmo salar* L. that survived the experimental period ($N = 315$), that were caught by the artificial predator in the morning ($N = 31$), that were caught by the artificial predator in the afternoon ($N = 6$) or that died of undefined causes ($N = 8$). Farm salmon were significantly larger than hybrid and wild salmon. Initial weight of individuals that were caught by the artificial predator was not significantly different to the initial weight of individuals that survived the experimental period. Individuals that died of undefined causes were in general smaller than individuals that survived the experiment or that were caught by the predator. Error bars show the standard error. Due to the lack of multiple observations some bars are presented without an error estimate. In these cases only one individual per family were caught by the artificial predator or died of undefined causes.

consideration, no difference in initial body weight was detected between individuals that survived the experiment and those that were caught by the artificial predator (Tables 3 and 4, Fig. 4).

The wild individuals that died of undefined causes during the experimental period were significantly smaller than the individuals that survived the experiment (Tables 3 and 4, Fig. 4). These individuals were also smaller

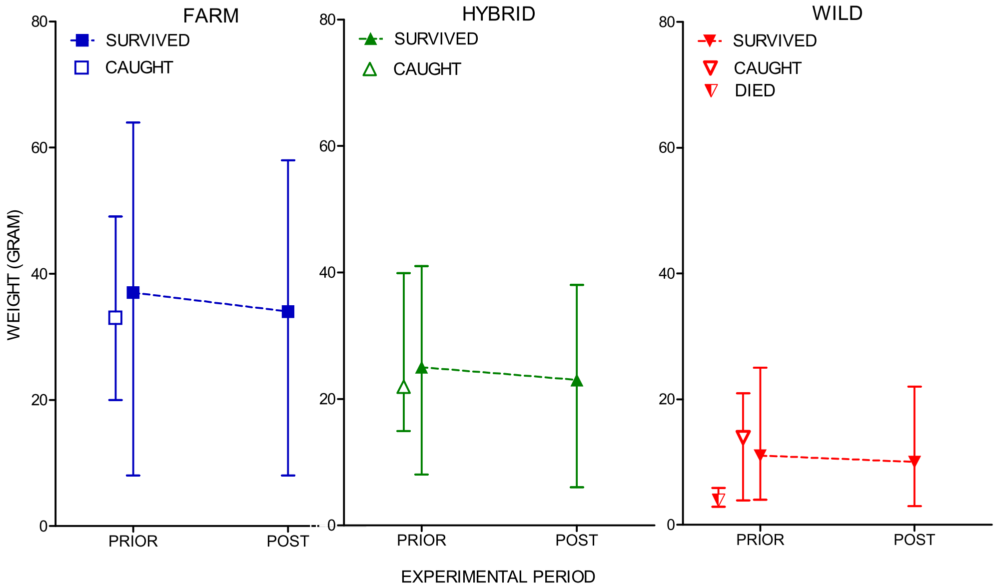

Fig. 5. Initial weights of wild, hybrid and farmed salmon and the growth reaction norm of salmon surviving the experiment. Mean strain weight prior to the experimental period of the farm, hybrid or wild Atlantic salmon *Salmo salar* L. that survived the experimental period ($N = 315$), that were caught the artificial predator ($N = 37$) or that died of undefined causes during the experiment ($N = 8$). For surviving salmon the negative growth reaction norm slope illustrates the response to competition for feed, i.e., a general reduction in body weight. Error bars show the range.

than the individuals caught by the artificial predator in the morning (Tables 3 and 4, Fig. 4). Even though all six individuals caught by the artificial predator in the afternoon, except one, were larger than the eight individuals that died of undefined causes, their initial weight was not significantly different (Tables 3 and 4). This was likely due to the small sample size.

Heterogeneity of variance in initial weight among families were detected and controlled for in the LME models (Table 1, Fig. 4), while heterogeneity of variance among the two replicated tanks were not detected (Table 1).

3.3. Predation susceptibility

Salmon of farmed, hybrid and wild origin were caught by the artificial predator in similar frequencies, both in the morning and in the afternoon, i.e., 10:11:10 and 2:2:2, respectively (Table 3, Fig. 3). Thus, susceptibility to the artificial predator was not origin-specific (Table 2). Furthermore, susceptibility to the artificial predator was not influenced by initial weight of salmon fry prior to the experimental period, i.e., susceptibility to the predator was not size-specific (Table 2). Heterogeneity of variance in survival between families and tanks were not detected.

3.4. Growth of surviving salmon

In general, all surviving salmon displayed a reduction in body weight during the experimental period (Table 3, Fig. 5). The calculated standardised mass-specific growth rate Ω (% per day) was similar in salmon of farmed, hybrid and wild origin (Table 1, Fig. 6). Thus, indicating a similar response to the nutritional competition in salmon of all origins. Heterogeneity of variance in Ω between families and tanks were detected and controlled for in the LME model (Table 1, Fig. 6).

4. Discussion

The main results of this study can be summarised as; (i) susceptibility to the artificial predator were similar in salmon of all origins, farm = hybrid = wild; (ii) susceptibility to the artificial predator was not size-selective; large individuals = small individuals; (iii) three weeks of nutritional competition resulted in a reduction in body weight in salmon of all origins, i.e., negative growth rates; (iv) surviving salmon of all origins displayed similar negative growth rates, i.e., similar growth response to competition for feed.

No difference in susceptibility to the artificial predator was detected in salmon fry of farmed, hybrid and wild origin when investigated together in a semi-natural environment with restricted access to feed. Theoretically, this may reflect that there is in fact no genetic difference between farmed and wild salmon in their susceptibility to predation. Alternatively, this result could reflect that the artificial predator and rearing conditions used in this experiment did not allow potential genetic differences in risk-taking behaviour between farmed and wild salmon to be revealed. These two possibilities are discussed below.

The choice of predator may have influenced these results. In general, few individuals were caught by the artificial predator, i.e., 37 out of 360 individuals. This could indicate that the warning signal given prior to the attack by the predator might have been too strong, resulting in all fish responding to the signal by fleeing the area while a

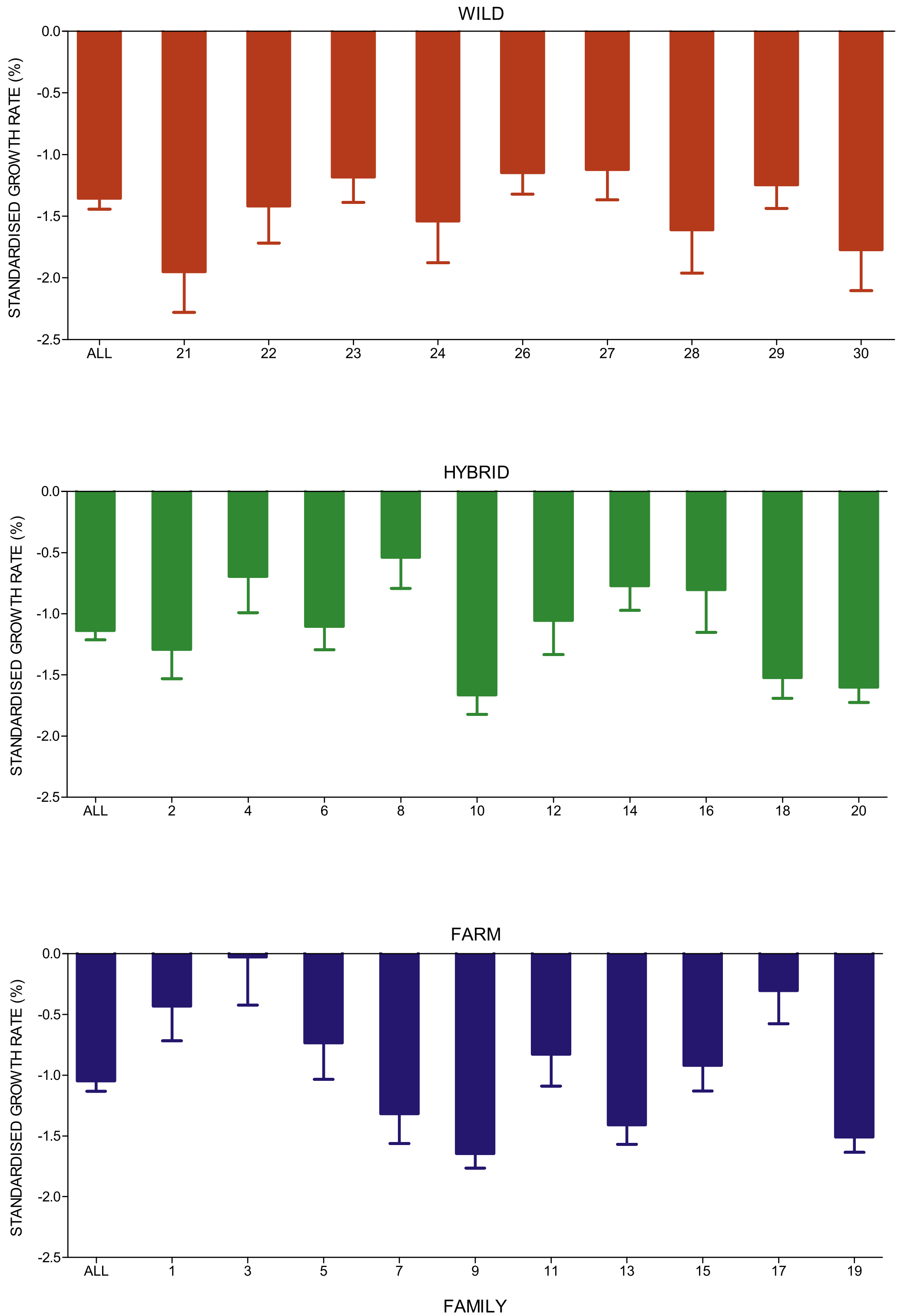

Fig. 6. Standardised mass-specific growth rate of surviving wild, hybrid and farmed salmon. Mean strain and family standardised mass-specific growth rate Ω (% per day) of the wild, hybrid and farmed Atlantic salmon *Salmo salar* L. that survived the experimental period ($N = 315$). Due to the restricted feeding ration and/or environmental stress, growth during the experimental period was in general negative. No difference in growth between salmon of farmed, hybrid and wild origin were detected. Error bars show the standard error.

few individuals were randomly caught by the predator. It also could indicate that the time gap between the warning signal and the actual attack was too long, giving both fast and slow responding salmon time to flee the area before the attack was initiated. Alternatively, the predator-system was too slow, giving most salmon the ability to escape the strike by the artificial predator. The low numbers caught by the artificial predator and the decrease over time could also indicate that salmon adapted to the predator-system, i.e., salmon were exposed to the artificial predator for two weeks (10 days in total), while ~60% of the individuals were caught within the first four days. After this point, individuals were not longer caught by the artificial predator in the afternoon, only in the morning after a 12 h period of starvation (which suggests hunger increases risk-taking behaviour). For those individuals that were caught by the artificial predator after day four, 4, 6 and 6 individuals were of farmed, hybrid and wild origin, respectively. Response to simulated predator attacks has previously been demonstrated to be inversely related to exposure in farmed and wild Atlantic salmon (Johnsson et al., 2001). Learning to avoid predation or other forms of danger has also been observed in fish (Kelley and Magurran, 2003; Klefoth et al., 2013).

The ambient environmental conditions could also have influenced these results. Restricted feed rations were provided during the experimental period, and negative growth rates were detected in salmon of all origins. A trade-off between energetic requirements and risk has been suggested in salmonids, e.g., anti-predator behaviour of juvenile Coho salmon *Oncorhynchus kisutc* decreased as both hunger level and competition level increased (Dill and Fraser, 1984). The restricted feeding rations in this study could have resulted in all fish prioritising feeding behaviour instead of anti-predator behaviour, masking any potential difference in susceptibility to the artificial predator in farmed, hybrid and wild salmon. The negative growth rates could also indicate that fish were not adapted to the experimental conditions. Reduced stress responsiveness has been documented in farmed relative to wild salmon (Solberg et al., 2013a). Only wild salmon died of undefined causes in this study, which could indicate that wild salmon perceived the experimental environment as more stressful than the farmed salmon. If so, the increased stress level could have impaired the wild salmon's ability to avoid the artificial predator.

The lack of a difference in susceptibility to the artificial predator in this experiment could indicate that there are no significant genetic differences in susceptibility to predation between salmon of wild and farmed origin. Our results are similar to a study from a natural river system where farmed, hybrid and wild salmon were planted out as eggs and sampled as prey in brown trout stomachs (Skaala et al., 2014). However, in the study by Skaala et al. (2014), salmon fry of farmed and hybrid origin were detected in a slightly higher number than fry of wild origin, although not significantly different. Offspring of farmed Norwegian salmon have been documented to display a higher risk-taking behaviour as compared to offspring of size matched wild salmon, by leaving cover sooner after a simulated predator attack by brown trout (Einum and Fleming, 1997). A stronger flight response were also detected in wild as compared to farmed salmon after exposure to a plastic heron head (Johnsson et al., 2001), although this result may have been influenced by wild salmon being closer to the model predator at the time of the attack (Johnsson et al., 2001). Canadian farmed and hybrid fry also left cover sooner than fry of wild origin after a simulated predator attack by belted kingfisher *Ceryle alcyon*, indicating a genetically higher risk-taking behaviour (Houde et al., 2010b).

Increased risk-taking behaviour has also been detected in domesticated/wild juvenile rainbow trout *Oncorhynchus mykiss* hybrids, as compared to their sized matched wild conspecifics (Johnsson and Abrahams, 1991). When given the option between foraging in a safe area and in an area where adult farmed rainbow trout were present, hybrids displayed increased willingness to forage in the unsafe area (Johnsson and Abrahams, 1991). However, when forced to encounter with adult rainbow trout, equal susceptibility to predation were documented in fry of both origins (Johnsson and Abrahams, 1991). Increased susceptibility to predation was however detected in hatchery reared rainbow trout as compared to size matched fry of wild origin, when subjected to predation by prickly sculpin *Cottus asper*, both under laboratory conditions and in a semi-natural stream (Berejikian, 1995). Offspring of domesticated rainbow trout also displayed lower survival, i.e., lower recapture rates, than offspring of wild trout when stocked in experimental lakes containing no natural fish populations, but at high risk of predation by birds (Biro et al., 2004). Interestingly, when predation risk was low or absent, domesticated rainbow trout displayed a higher survival than wild trout, although this difference was only marginal at low risk of predation (Biro et al., 2004).

Increased susceptibility to predation has thus far not been demonstrated in farmed Atlantic salmon, and the suggested link between the documented risk-taking behaviour and susceptibility to predation still remains to be elucidated in order to understand if behavioural differences between farmed and wild salmon could, partially, explain why offspring of farmed salmon display lower survival in the wild (McGinnity et al., 1997, 2003; Fleming et al., 2000; Skaala et al., 2012).

In this study, susceptibility to the artificial predator was neither origin- nor size-specific. As individuals were randomly caught by the predator and not according to size, the relative difference in weight between wild and farmed salmon was similar before and after exposure to the artificial predator. Weight measurements taken prior to the experimental period showed that wild salmon were outgrown by farmed salmon by 3.13:1, while the adjoining numbers of surviving salmon post the experimental period were similar at 3.18:1. The relative difference in weight between farmed and wild salmon at the fresh water stage has been documented to be small in the wild, e.g., in River Guddal offspring of farmed salmon outgrew offspring of wild salmon at a maximum of 1.25:1 at the smolt stage (Skaala et al., 2012). Furthermore, we have previously demonstrated that the relative difference in weight between farmed and wild salmon decreased when competition and mortality levels increased along an environmental gradient approaching natural conditions

(Solberg et al., 2013b). Our previous study, based upon the same genetic material as included in this study, were performed along an environmental gradient without predation. Based upon the documentation of increased aggressiveness and risk-taking behaviour in farmed salmon (Einum and Fleming, 1997; Fleming and Einum, 1997; Houde et al., 2010a,b), we hypothesised that size-selective predation induced mortality towards the fastest growing farmed salmon might be pushing the observed growth rate of surviving farmed salmon further towards the observed growth rate of wild salmon in nature. However, positive size-selective mortality towards farmed salmon was not detected in this study, as salmon of all sizes were equally captured by the artificial predator.

Individual growth rates were calculated for all surviving individuals, while controlling for their initial body size. As some of the individuals included in this study were too small to be physically tagged, thus ruling out that option, individual weight measurements prior to and post the experimental period were matched by the use of individual DNA profiling. All salmon displayed negative growth rates, i.e., a decrease in body weight due to the restricted feed ration and/or the environmental conditions provided during the experimental period. Furthermore, no difference in growth rate was detected between salmon of farmed, hybrid and wild origin, indicating that the response to competition for food was similar in salmon of all origins under these experimental conditions.

Farmed salmon has for commercial reasons been selected for increased growth for approximately ten generations (Gjedrem, 2000; Thodesen and Gjedrem, 2006; Glover et al., 2009), while in the wild growth rate is an important trait for early survival and fitness (Roff, 1984). Successful introgression of farmed salmon has been documented in the wild (Crozier, 1993, 2000; Clifford et al., 1998a,b; Skaala et al., 2006; Bourret et al., 2011; Glover et al., 2012, 2013), even though the fitness related consequence of introgression in native populations is still a matter of debate. However, increased mortality of salmon of farmed origin in nature (McGinnity et al., 1997, 2003; Fleming et al., 2000; Skaala et al., 2012) indicates that introgression is not likely to inflict a positive fitness effect upon the wild population. Thus for conservational reasons, elucidating genetic differences in behaviour and growth of farmed and wild salmon is an important step towards understanding the ecological consequence of farmed salmon introgressing in wild populations. This study illustrates how DNA-based individual identification can be used as a tool to investigate trait expressions over time in young individuals too small to be tagged. Thus, opening up for comparative studies of early life history traits of farmed and wild salmon, not only at the strain or family level, but at the individual level.

5. Conclusions

Under the experimental conditions of this study, salmon of farmed, hybrid and wild origin displayed equal susceptibility to an artificial predator. Higher susceptibility to predation through altered risk-taking behaviour has been suggested as a partial explanation as to why offspring of farmed salmon display a lower survival in nature as compared to offspring of wild salmon. However, the link between risk-taking behaviour and susceptibility to predation has yet to be demonstrated in Atlantic salmon, together with the underlying mechanisms causing the offspring of farmed salmon to display lower survival in the wild as compared to offspring of wild salmon.

Conflict of interest

None declared.

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